Whales, Whaling and Ecosystem Change in the Antarctic and Eastern Bering Sea: Insights from Ecosystem Models

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The question of whether species assemblages are controlled by food availability or by predators is a fundamental ecological question that has implications for biological conservation, maintenance of biodiversity, development of marine protected areas, and management of economically and culturally important marine resources (Worm and Duffy, 2003). Increases in prey populations following the removal of predators by fisheries have been taken as proof that top-down processes control marine ecosystems (e.g., Worm and Myers, 2003). Similar arguments have been used to justify perceived benefits of whaling to fisheries (e.g., Tamura, 2003), or to account for large scale ecosystem changes noted in the northern and southern hemispheres following the cessation of whaling (e.g., Knox, 1994; Springer *et al.,* 2003).

There is considerable uncertainty about the role that whales play in the ecosystem. Many of the large-scale changes noted in marine ecosystems have been attributed to the effects of human activities, especially commercial whaling. One such example is the compelling and eloquently simple hypothesis proposed by Springer *et al*. (2003) to explain a cascading series of population declines that began in the late 1970s in the Gulf of Alaska, Aleutian Islands and Bering Sea. The core of their argument is that killer whales (*Orcinus orca*) were forced to eat smaller marine mammals after commercial whalers wiped out the fin, sei and sperm whales within 370 kilometers of the Alaskan coastline between 1949 and 1969. The end of whaling was soon followed by the crash of harbor seals, northern fur seals, and Steller sea lions through the late 1970s and 1980s (Pitcher, 1990; Trites, 1992; Trites and Larkin, 1996). This in turn was followed by the decline of sea otters in the 1990s (Estes *et al.,* 1998; Doroff *et al.,* 2003). Killer whales, it is theorized, had little choice but to eat their way through the top trophic levels of the North Pacific, leaving critically low populations in their wakes (Springer *et al.,* 2003).

An equally compelling hypothesis has been proposed to explain population dynamics at the opposite end of the world — the Southern Ocean (Knox, 1994; Berkman, 2002). Many Antarctic species were reduced by sealing in the late 1700s and early 1800s (Bonner, 1982; Knox, 1994), and by whaling in the first half of the 1900s (May, 1979; Berkman, 2002), and then by fishing in the mid 1900s (Kock, 1992). Numbers of some species have since increased (e.g., penguins and Antarctic fur seals; Bonner, 1976; Croxall, 1983; Williams, 1995; Boyd, 2002), but others such as the large whale species have not recovered (Kasamatsu and Joyce, 1995; Kasamatsu *et al.,* 2000). Increases in Antarctic fur seal populations through the 1950s–1990s may have been due to the removal of competitors by whaling during the first half of the 20th century, or by the finfish fishery in the late 1960s and early 1970s.

Evaluating the hypotheses concerning the effects of whaling on ecosystems is difficult given the lack of experimental controls or suitable ecological systems with which to compare them. However, it is possible to quantitatively evaluate the hypotheses using mathematical models that capture the essence and logic of their arguments. Ecosystem models are one means of synthesizing current understanding about food webs and interactions between species to determine whether the removal of species could have the expected outcome.

Two ecosystem models were recently constructed to test whether large whales played a significant role in structuring the dynamics of the Bering Sea and the Antarctic marine ecosystem (Trites *et al.,* 1999a; Bredesen, 2003). Both studies used Ecopath modeling software (Polovina, 1984; Christensen and Pauly, 1992), a widely employed program that provides a framework for describing food webs and tracking the flow of biomass through them. They also used Ecosim, a dynamic component of Ecopath that is capable of simulating ecosystem changes over time (Walters *et al.,* 1997). Ecopath and Ecosim represent all of the major components of the ecosystem and their feeding interactions, but are relatively simple. Ecopath estimates the trophic position of each species or group of species within an ecosystem, and provides a means of assessing the main effects that species such as cetaceans might have on the food web and the overall structure or composition of the ecosystem. These kinds of models readily lend themselves to exploring simple, ecosystem-wide questions about the dynamics and the response of the ecosystem to anthropogenic changes.

This paper reviews the findings of the recent Bering Sea and Antarctic ecosystem models to better understand the role that cetaceans play in marine ecosystems.

THE EASTERN BERING SEA

Ecopath models were constructed by Trites *et al*. (1999a) for the shelf and slope regions covered by the Alaska Fisheries Science Center's bottom trawl surveys (Figure 1). They encompassed two periods: (a) the '1950s' covering the years 1955 to 1960, before large-scale commercial fisheries were underway, and (b) the '1980s' covering the period 1979-1985, after many marine mammal populations had declined. Both were annual average models, which means that the biomass, together with the diets and species composition of summer and winter, were averaged to provide a year round 'annual average'. Biologically similar species were grouped into 'functional groups' (Figure 2), and input parameters were gathered from the literature, including biomass, rate of production, rate of consumption, and diet composition for the groups in the system (Trites *et al.,* 1999a and Coombs and Trites, unpubl. data). The seven marine mammal groups included: 1. baleen whales (fin, minke, blue, humpback, bowhead, northern right, gray)*;* 2. sperm whales; 3. toothed whales (beluga, killer, Dall's porpoise, harbour porpoise)*;* 4. beaked whales; 5. Pacific walrus and bearded seals; 6. Steller sea lions; and 7. seals (northern fur seal, harbour seal, spotted seal, ribbon seal, and ringed seal).

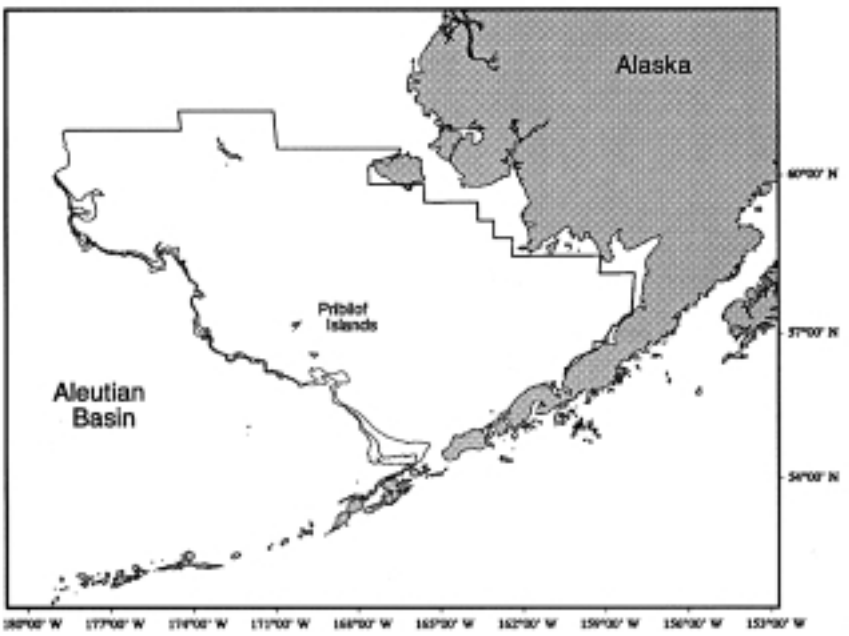

Fig. 1. The eastern Bering Sea as defined in the ecosystem model. Total area is approximately 500,000 km^2.

A flowchart showing trophic interactions and energy flow in the eastern Bering Sea during the 1980s is presented in Figure 2. The flow chart depicting the 1950s ecosystem is similar in layout to the 1980s flowchart, containing the same species at roughly the same trophic levels. Where the two systems differ is in the relative sizes of the boxes (i.e., in the biomass of the different functional groups). Large flows of energy in the Bering Sea emanated from three species at trophic level III – pelagic fishes in the 1950s and pollock and small flatfish in the 1980s. The major consumers (top predators—trophic level IV) included the marine mammals and birds, as well as large flatfish and deepwater fish.

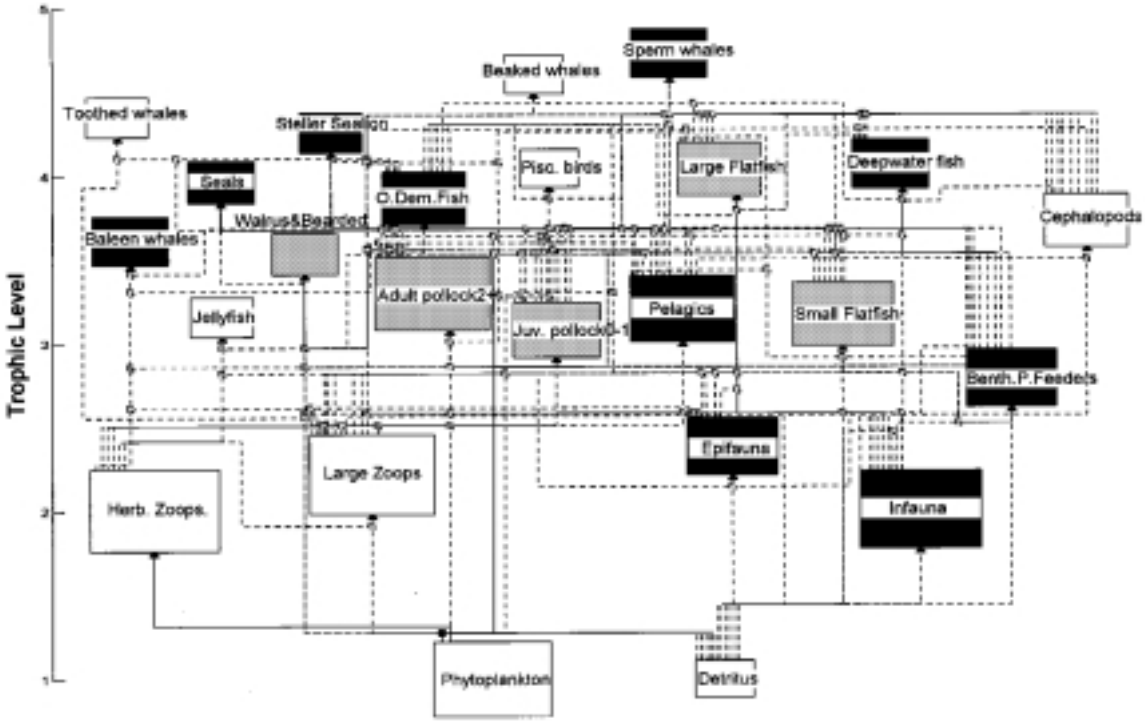

Fig. 2. Flowchart of trophic interactions in the eastern Bering Sea during the 1980s. The blackened boxes indicate which groups had lower estimated abundance in the 1980s than in the 1950s, and the shaded boxes show which species were estimated to have higher abundance in the 1980s than in the 1950s. Connecting lines show the major trophic flows of energy between functional groups (minor flows are omitted).

Niche overlaps were calculated between pollock, large flatfish and marine mammals in the 1980s model using two approaches. One determined the extent to which any two groups sought the same prey (referred to as prey overlap). The other approach determined to what extent they were subject to predation by the same predators (predator overlap).

In terms of which species sought the same prey in the Bering Sea, baleen whales and pollock (both adult and juvenile) had the greatest dietary overlaps (68-83%). There was also substantial overlap between seals and adult pollock, and between seals, sea lions and flatfish. Diets of toothed whales overlapped primarily with that of beaked whales and seals, while adult pollock shared a large proportion of their diet with juvenile pollock. The largest potential competitors of sea lions appeared to be seals, toothed whales and large flatfish.

Removing baleen whales from the 1950s Bering Sea model increased the toothed whales, sperm whales, beaked whales, walrus, bearded seals, seals, sea lions and sea birds (Figure 3). Reducing baleen whales also increased zooplankton biomass (reduced predation) and increased their major competitors (pollock and cephalopods), which were consumed by other marine mammals. However, none of the increases were particularly large (i.e., most were <10%). Removing baleen whales had a positive effect on pollock and seals (northern fur seals, harbour seals, spotted seals, ribbon seals and ringed seals), but no discernable effect on pelagic fishes or sea lions.

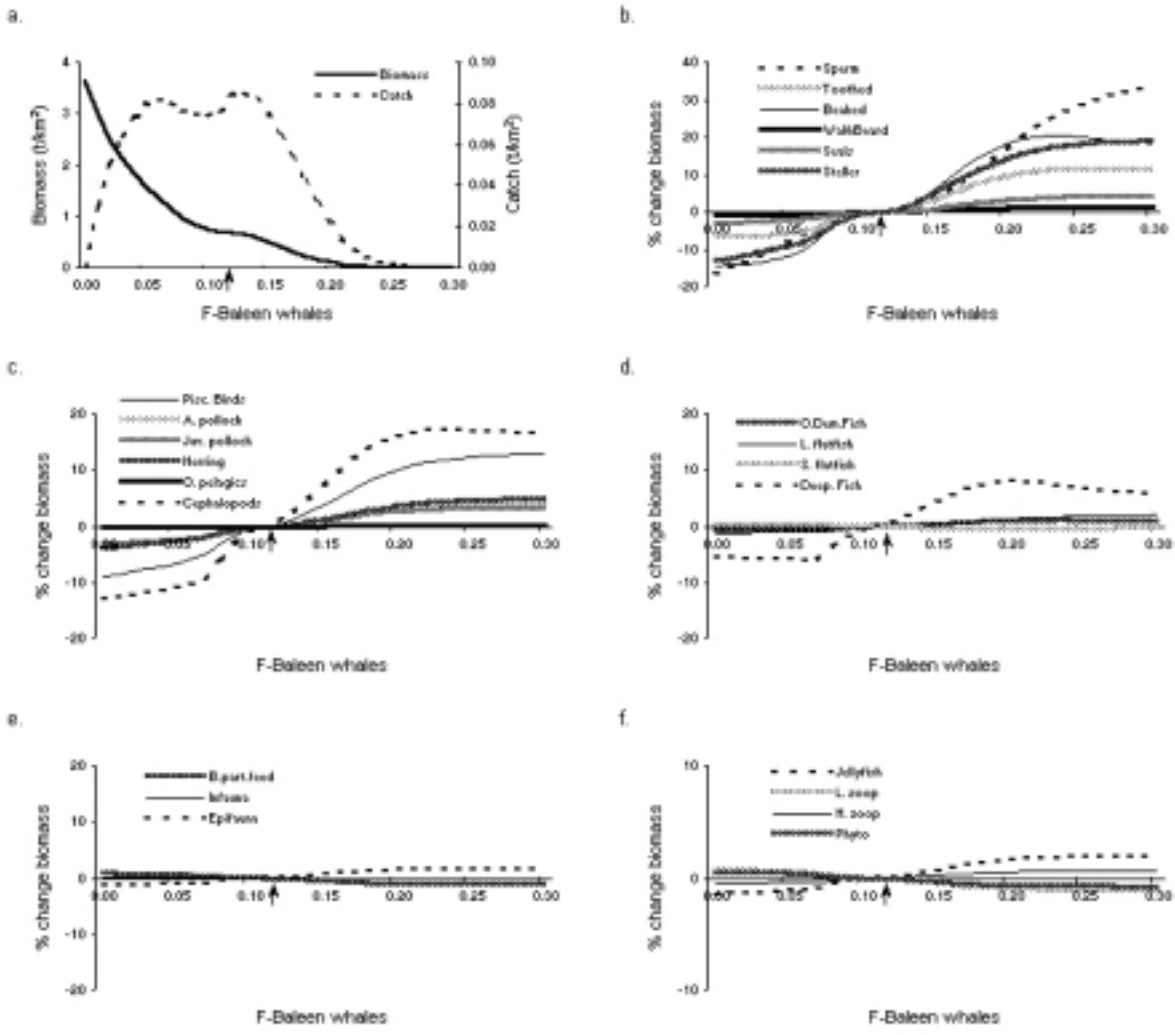

Fig. 3. Equilibrium biomass for Bering Sea species following changes to the fishing mortality of baleen whales in the 1950s model. Arrows mark the instantaneous rate of fishing (F‡year^{-1}) during the 1950s. The top left panel shows changes in the biomass and catch of baleen whales under different levels of F. The other five panels show the relative change (%) that could occur to other species in the ecosystem to compensate for changes in the abundance of baleen whales (at different levels of F shown in panel a).

The model predicted that increases of baleen whales in the eastern Bering Sea could reduce the abundance of pollock, cephalopods and deepwater fishes through direct competition for zooplankton. However, changes in the biomass of marine mammals appear to have little effect on the biomass of other groups in the Bering Sea (Figures 3 and 4). Removing baleen whales resulted in less than a 10% change in biomass of other groups after 100 years of simulation (Figure 4), with the exceptions of beaked whales (22% increase after 100 y), cephalopods (20%), Steller sea lions (16%), deepwater fish (12%), and toothed whales (11%). Overall, reductions in prey abundance can quickly reduce marine mammal populations, but marine mammals are unable to quickly recover when abundant food becomes available.

Commercial whaling and fishing activities had little effect on the simulated ecosystem. Fishing (i.e., killing whales and catching fish) failed to account for the large abundance of pollock and the decreased population sizes of seals and sea lions observed in the 1980s. It therefore seems unlikely that whaling could have unleashed the ecosystem-wide changes purported by Springer *et al*. (2003).

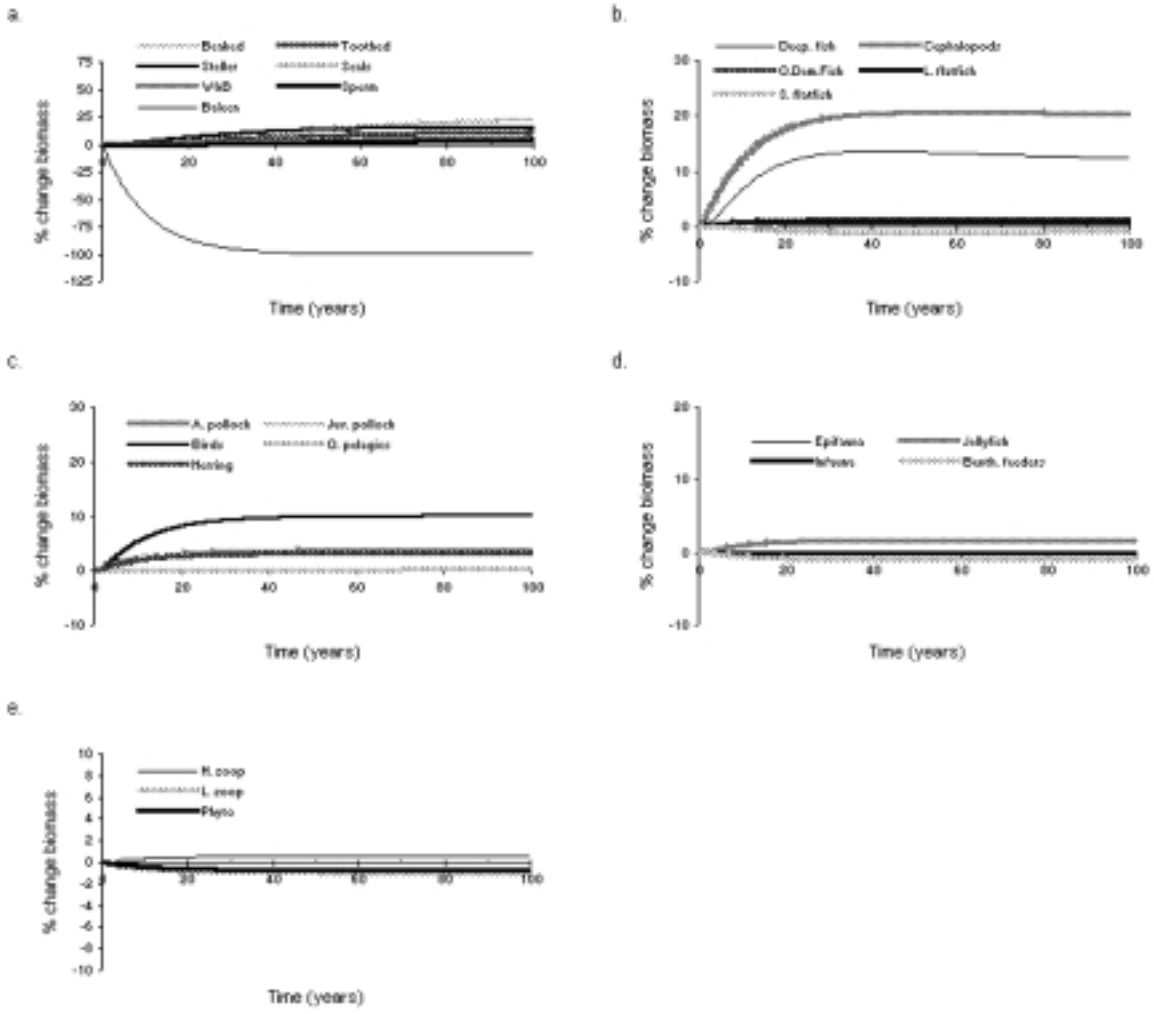

Fig. 4. Dynamic simulation of the effects of commercial fishing for 100 years starting in the 1950s. Note that some predators switched from eating pelagic fishes to eating pollock.

THE ANTARCTIC

The region of the Antarctic that was modeled included the South Orkney Islands and the Island of South Georgia (Figure 5). This South Orkneys/South Georgia region has been subjected to both historical and present-day exploitation, and supports large populations of top predators, including pinnipeds, seabirds, and baleen whales (Knox, 1994). Over 200 species of plankton, invertebrates, fish, birds, seals and whales feed and/or breed in the South Orkneys/South Georgia region. These organisms were classified into 29 functional groups. Detailed descriptions of the groups, data sources for all model parameters, and model outputs are contained in Bredesen (2003).

Two models were constructed to address questions concerning ecosystem interactions and the role of large whales. The first model represented the 1900s (i.e., after the extensive hunting of pinnipeds had ceased, but before whaling began), and was used to explore the effects of removing whales from the ecosystem. The second model, corresponding to the 1990s (i.e., present-day), was used to address the recovery of whale populations. Biomass during the 1990s was dominated by krill and other zooplankton, while whales, seals and birds contributed relatively little to the overall biomass of the ecosystem (Figure 6).

The whaling activities of the first half of the 20th century were simulated by removing 10% of the baleen whales from the 1900s model each year from 1900 to 1950. This was followed by 50

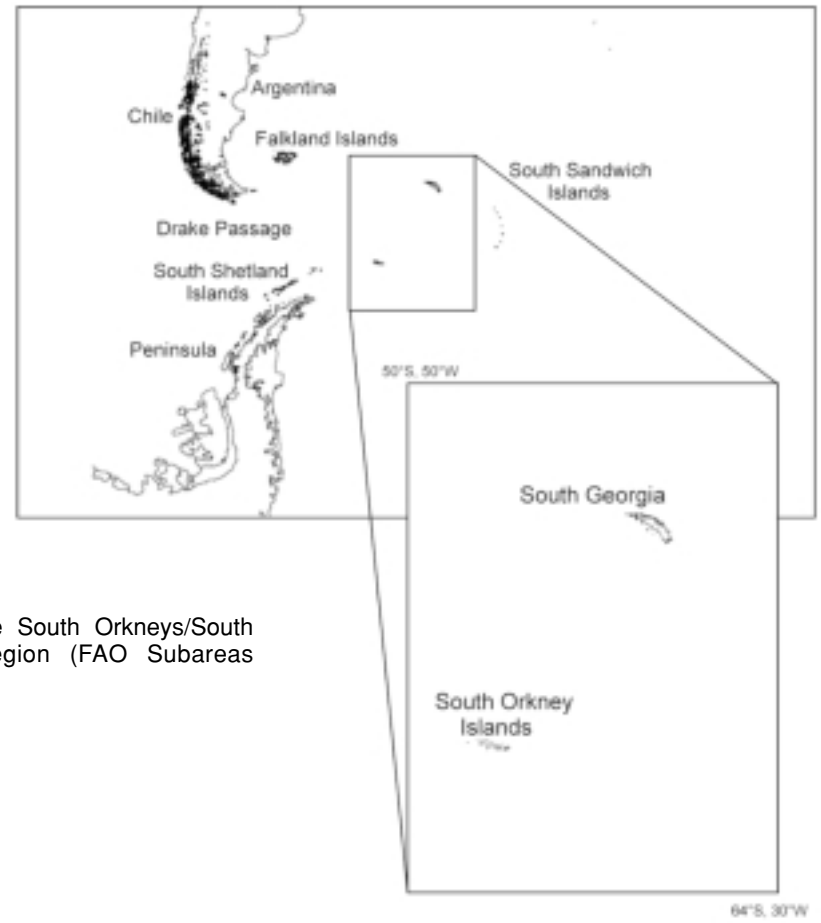

Fig. 5. The South Orkneys/South Georgia region (FAO Subareas 48.2, 48.3).

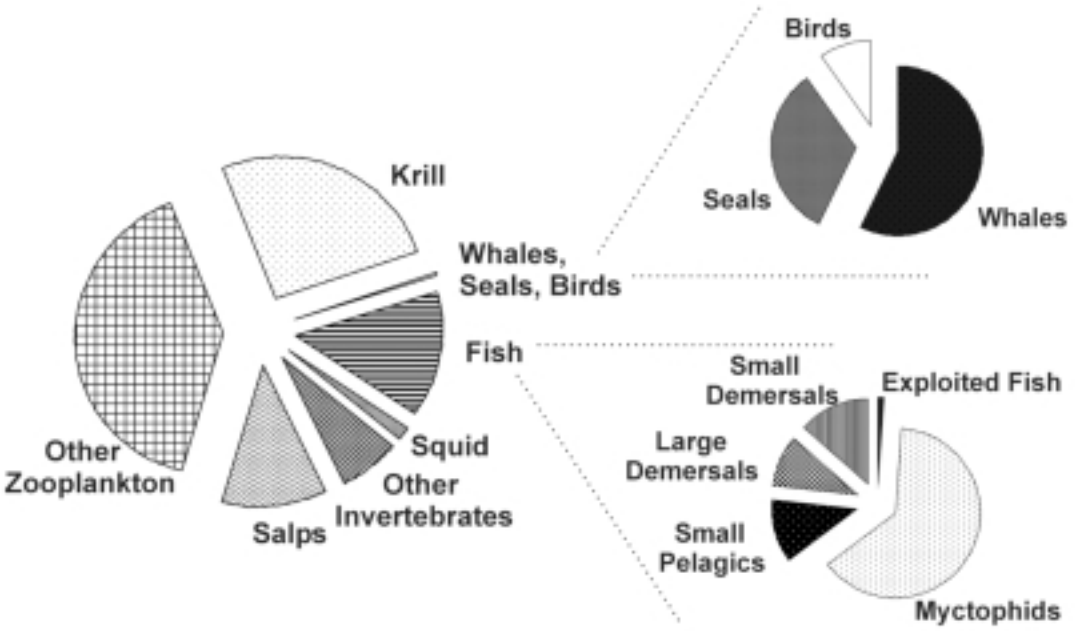

Fig. 6. The proportion of organisms (biomass) in the South Orkneys/South Georgia ecosystem in the 1990s. Exploited fish refers to the three main species that have experienced intense fishing pressure in the past (i.e., marbled rockcod, mackerel icefish and toothfish).

years of no whaling. This simulated hunt resulted in increases among some commercially important fish species (e.g., marbled rockcod, toothfish and mackerel icefish; Figure 7). However, the biomass of Antarctic fur seals did not increase, in contrast to the observed trend of Antarctic fur seal populations over the last century (Payne, 1977; Boveng *et al.,* 1998). Removing 10% of the baleen whale biomass each year reduced the biomass of the simulated whale population to about 5% of its original size in about 50 years. Cessation of whaling (after removing 10% for 50 years) resulted in whale biomass recovering to only about 10% of its original biomass at the end of 100 years of simulation.

Attempts to enhance the recovery of large whales were explored by 'culling' other species in the ecosystem. Running the 1990s model forward with a simulated cull of certain species (e.g., removing 10% of the biomass annually for the duration of a 100-year simulation) provided insights into the factors that influence whale abundance. Model results showed that culling Antarctic fur seals increased penguin and crabeater seal biomass, while culling both Antarctic fur seals and crabeater seals increased penguin biomass even more. A simulated cull of penguins resulted in a positive response in baleen whale populations — although even then, the model only indicated a 10% increase in overall whale biomass after 100 years of culling. The model suggested that the greatest increase in baleen whale biomass would result from a cull of myctophids, which would increase whale biomass by 40% over the 100-year time period. However, reducing myctophid biomass negatively affected other species, such as Weddell seals and king penguins.

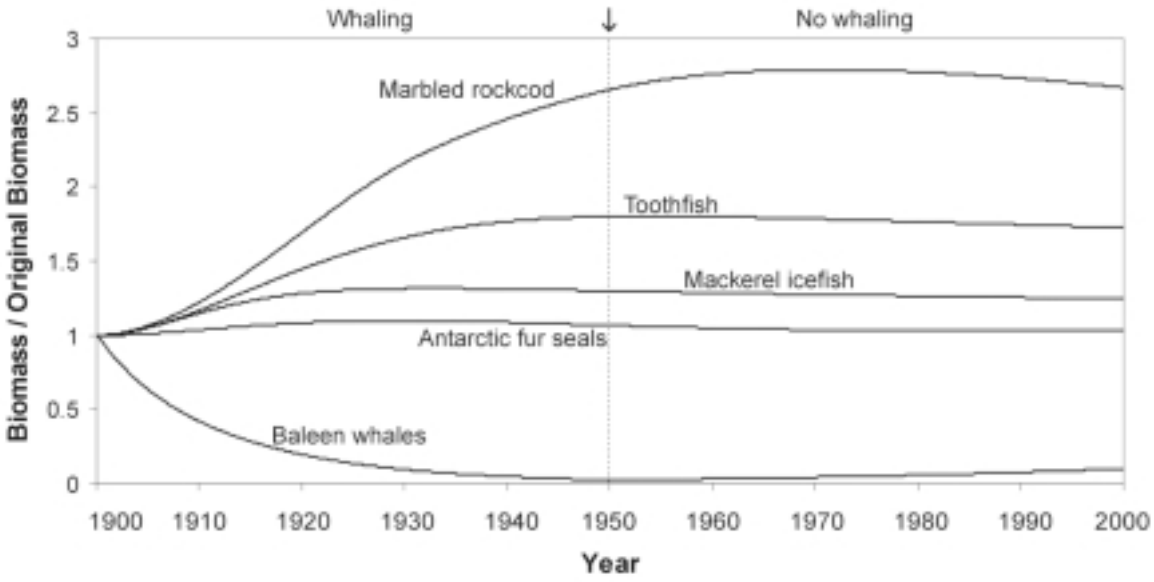

Fig. 7. Predicted biomass changes of several species in response to simulated whaling. Ten percent of baleen whales were removed from the modeled ecosystem each year from 1900 to 1950, followed by 50 years of no whaling.

CONCLUSIONS

The ecosystem models constructed for the Antarctic and the Bering Sea incorporate current understanding of biological interactions of species within the ecosystem (i.e., who eats whom and how much; Trites, 2003). Within the limitations that are inherent to simulations, both models suggest that removal of large whales had little measurable effect on lower trophic levels or on the dynamics of other species in their polar ecosystems.

Trophic interactions failed to explain the magnitude of changes in the biomass of the major species groups in the Antarctic and Bering Sea. Nor did fin-fisheries appear to have had a significant effect on the abundance of non-targeted species. This may mean that environmental effects (which were not modeled) play an important role in influencing the dynamics of marine ecosystems. Oceanographic factors such as changes in water temperature or ocean currents like-

ly result in variations in ecosystem production and species recruitment patterns which are not captured by our Ecopath models (Trites *et al.,* 1999b).

The Ecopath modeling approach is a powerful means of synthesizing knowledge about ecosystems and the factors that influence ecosystem dynamics. They provide a straightforward means for estimating trophic levels and niche overlaps with other species to assess the potential for resource competition. While the models failed to support the hypotheses that large whales play a significant structural role in the Antarctic and Bering Sea ecosystems, they do support what most already know — i.e., that populations of large whales are easily reduced to low numbers, but take a long, long time to recover. They also help in recognizing the need to consider factors other than food web interactions when assessing the status of cetaceans, as well as highlighting the potential tradeoffs that can result when other species are removed from ecosystems.

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